PAN-PACIFIC ENTOMOLOGIST
67(3): 189–194, (1991)

DEVELOPMENT AND SURVIVORSHIP OF *CYDIA POMONELLA* (L.) (LEPIDOPTERA: TORTRICIDAE) AT TEN CONSTANT TEMPERATURES

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Abstract.—Development and survivorship of *Cydia pomonella* (L.) immature stages were observed at 10 constant temperatures between 8.9° and 34.4° C. All stages failed to complete development at temperatures below 12.2° C. Fourteen percent of the eggs and no larvae or pupae survived at 34.4° C. The lower developmental thresholds, estimated by regressing developmental rate (1/days) against temperature, ranged between 10.5°–12.5° C. A nonlinear model based on Logan's function was fit to the observed data and provides a more complete description of the developmental rate-temperature relationship than a linear model.

Key Words.—Insecta, *Cydia pomonella,* developmental rates, threshold temperatures, Logan's model

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Cydia pomonella (L.), codling moth, is the most destructive insect pest of walnuts, apples, pears and plums in California. Damage is caused by larvae feeding directly on fruit resulting in early fruit drop or unmarketable mature fruit (University of California in press). In the absence of effective biological and cultural controls, damage is prevented by properly timed insecticidal treatments. Spray timing is usually achieved using a degree-day model and pheromone trap catch data (Riedl et al. 1976; University of California 1987, in press).

The relationship between temperature and development of *C. pomonella* has been the subject of several studies (Glenn 1922, Shelford 1927, Hagley 1972, Williams & McDonald 1982, Rock & Shaffer 1983). Early studies were performed in an outdoor insectary under ambient air temperatures; later studies used constant temperature cabinets. However, all these studies investigated temperatures in the middle of the developmental rate curve, a portion that can be reasonably approximated by a straight line. For example, Rock & Shaffer (1983) reared larvae and pupae of moths collected in North Carolina at 16°, 22°, 28°, and 32° C. The lower thermal threshold (9.9° C) was estimated by regressing developmental rate against temperature; the upper thermal threshold was suggested to occur above 32° C.

Studies have shown that the relationship between codling moth developmental rate and temperature is significantly nonlinear (Rock & Shaffer 1983, Gold et al. 1987). Recent field studies in California showed that development under high summer temperatures (>30°C) was slower than predicted using a linear degree-day model (MJP & FGZ, unpublished data). We suggest that a nonlinear model may better represent moth development, especially when temperatures routinely exceed the upper thermal threshold. Here, we examine the rate of immature

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development of *C. pomonella* at 10 constant temperatures to provide a more complete description of its developmental rate curve and fit a nonlinear model to the data.

Materials and Methods

Cydia pomonella larvae, pupae, and adults were selected from a laboratory colony maintained on artificial diet (modified after Vanderzant & Davich 1958) at about 23° C and natural photoperiod. The colony was initiated with adults collected in apple orchards near Placerville, California. Eggs were obtained by placing 20 adult pairs in a metal rotating oviposition cage (Batiste & Olson 1973) 2–3 h before sunset; eggs were collected 4 h later and put into a vegetable crisper at 100% RH and immediately placed into a temperature cabinet. Sample size varied from 42–89 eggs.

Developing larvae were maintained individually on artificial diet (approximately 10 ml) in 30 ml plastic cups. The end of the larval stage was when larvae began to spin a cocoon. Pupal development was examined using individuals that started cocoons on the same day.

Ten constant temperature regimes were used: 8.9°, 10.0°, 11.1°, 12.2°, 15.6°, 25.6°, 27.8°, 30.0°, and 34.4° C. At 15.6° C and above, egg hatch was checked every 24 h; at 12.2° C and below, egg hatch was checked at 1–3 day intervals. Larvae and pupae were examined for completion of their developmental stage every 1–2 days at 15.6° C and above, and at 1–3 day intervals at temperatures below 15.6° C. The end of a stage was recorded as the midpoint between two observations.

The relationship between temperature and developmental rate (rate = 1/days) was described by linear and nonlinear regression models. Parameter estimates of the linear model were calculated by regressing observations at 15.6°–32.2° C (the X-intercept method of Arnold 1959). Parameter estimates of the nonlinear model were calculated using Marquardt's method of least-squares (SAS Institute 1985).

Results and Discussion

The survivorship and mean duration of development for the egg, larval, and pupal stages are presented in Table 1. Development was not observed in any stages at 8.9° and 10.0° C but was noted in all stages at 11.1° and 12.2° C. Eggs maintained at 8.9° and 10.0° C remained in the opaque white stage (Richardson et al. 1982), but those at 11.1° and 12.2° C developed to the blackhead stage and then died. Hagley (1972) studied the development of *C. pomonella* eggs at several constant temperatures, and reported that while all eggs failed to hatch at 10.0° C, 27% developed to the blackhead stage before dying. Successful egg hatch, however, did occur at 11° C. In our study, egg survival was highest between 15.6°–27.8° C, was lower at 30.0°–32.2° C and substantially lower at 34.4° C. These results corroborate Hagley's (1972) observations of reduced egg hatch at temperatures above 30° C. Larval survivorship in our study was >80% between 27.8°–32.2° C; pupal survivorship was >80% between 27.8°–30.0° C. No larvae or pupae survived at 34.4° C.

The number of days required to complete embryogenesis declined between 15.6°–27.8° C then increased with increasing temperature. For the larval stage, there was a general increase in developmental rate with increasing temperatures

Table 1. Survivorship and mean days required for development of immature stages of *Cydia pomonella* at different constant temperatures.

	Stage													
	Egg				Larva				Pupa				Total
Temperature (°C)	*n*[a]	S[b] (%)	Development (mean days ± SE)	Range (days)	*n*	S (%)	Development (mean days ± SE)	Range (days)	*n*	S (%)	Development (mean days ± SE)	Range (days)	Development (mean days)
8.9	75	0.0	—	—	30	0.0	—	—	20	0.0	—	—	—
10.0	73	0.0	—	—	30	0.0	—	—	20	0.0	—	—	—
11.1	78	0.0	—	—	30	0.0	—	—	20	0.0	—	—	—
12.2	80	0.0	—	—	30	0.0	—	—	20	0.0	—	—	—
15.6	89	77.5	19.26 ± 0.55	18.0–20.5	30	53.3	62.21 ± 2.75	54–82	20	25.0	68.18 ± 1.36	66–75	149.65
25.6	61	78.7	6.47 ± 0.42	5.0–7.0	30	76.7	17.14 ± 0.53	15–23	18	61.1	17.32 ± 0.56	15–21	40.93
27.8	64	79.7	4.21 ± 0.00	—	30	83.3	13.42 ± 0.22	11–17	19	89.5	10.10 ± 0.34	9–14	27.73
30.0	63	58.7	4.27 ± 0.33	3.5–5.5	23	87.0	14.68 ± 0.41	12–19	20	80.0	10.85 ± 0.58	7–15	29.80
32.2	75	49.3	4.56 ± 0.23	4.0–5.0	30	80.0	11.27 ± 0.25	11–14	18	22.2	10.71 ± 1.34	8–14	26.54
34.4	42	14.3	5.40 ± 0.57	5.0–6.0	30	0.0	—	—	30	0.0	—	—	—

[a] Sample size.
[b] Survivorship.

Table 2. Linear regression equations and estimates of lower developmental thresholds using mean developmental rates for immature stages of *Cydia pomonella*.

Stage	Regression equation[a]	SE of regression coefficient	r^2	Lower threshold[b] (°C)
Egg	Y = −0.121 + 0.0115*X	0.0024	0.88	10.56
Larva	Y = −0.048 + 0.0042*X	0.0005	0.96	11.54
Pupa	Y = −0.065 + 0.0052*X	0.0011	0.89	12.49
Egg-to-Adult	Y = −0.023 + 0.0019*X	0.0003	0.94	11.85

[a] Regression equation is Y = a + bX, where Y is the developmental rate (1/days) and X is temperature (°C).
[b] X-intercept.

above 15.6° C, the fastest rate occurring at 32.2° C. Little change in the rate of pupal development was observed at 27.8°–32.2° C. These results suggest that the upper developmental thresholds are near 27.8° C for the egg and pupal stages, and 32.2° C for the larval stage.

The estimated lower thermal thresholds and associated linear regression equations are presented in Table 2. The coefficient of determination, r^2, was high for all stages. Estimates of the lower thermal threshold ranged between 10.5°–12.5° C and are similar (or slightly lower) to the minimum temperatures for which development was observed. The average number of degree-days (° D) above the estimated threshold of 11.85° C for total development (egg to adult) is 529.45° D.

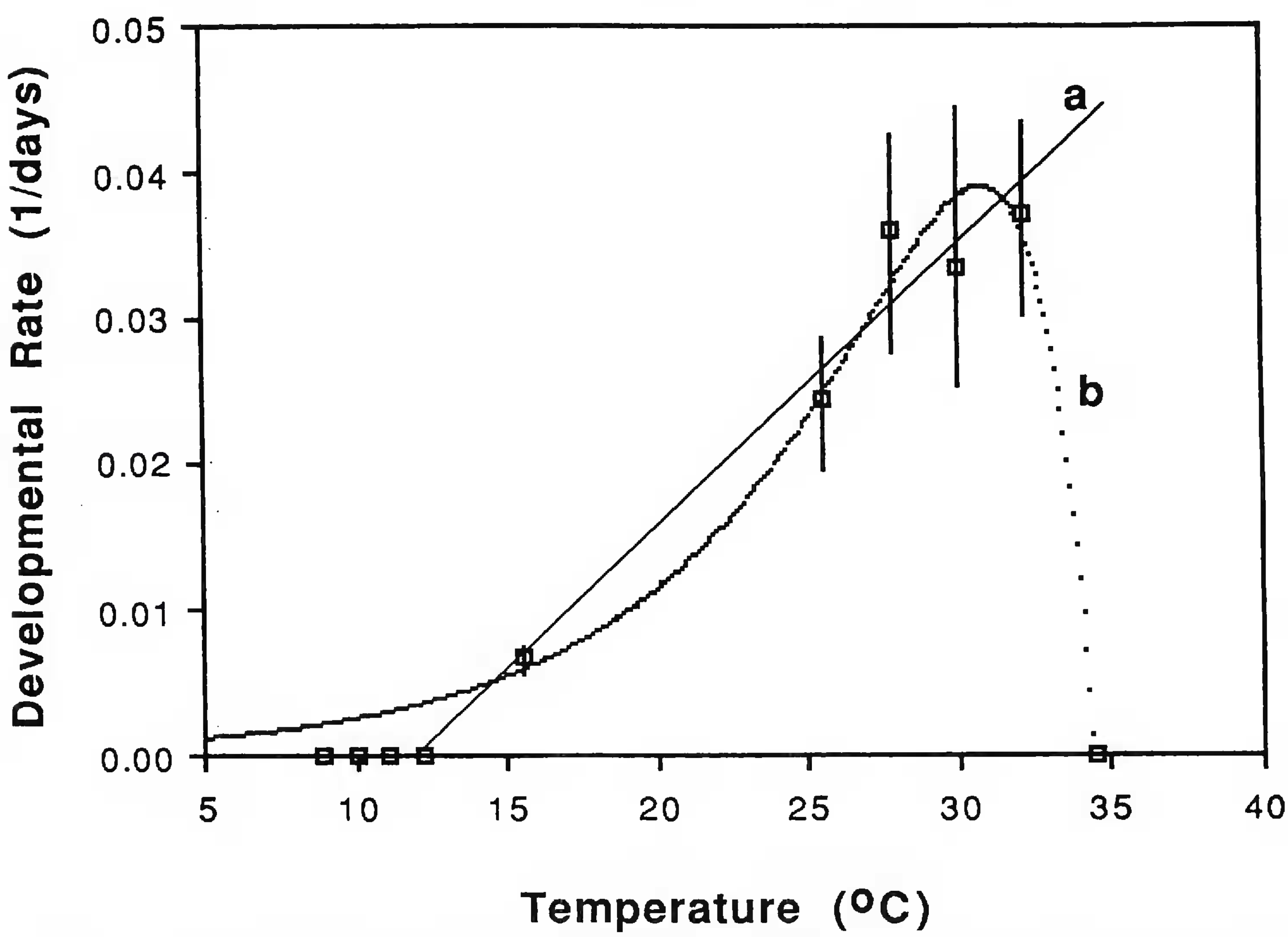

Figure 1. Rate of total (egg to adult) development as a function of temperature for *Cydia pomonella* (a = linear regression for the temperature range of 15.6–32.2° C; b = nonlinear model after Logan et al. 1976; means are given with range of observed values; parameter estimates are given in Tables 2 and 3).

Table 3. Parameter estimates of Logan's model to describe the relationship between *Cydia pomonella* developmental rate and temperature. In the model, rate = a{exp[b•x] − exp[b•c − (c − x)/d]}.

Life stage	Parameter estimates				df[a]
	a	b	c	d	
Eggs	0.0767	0.1921	36.1601	5.1617	265
Larvae	0.0036	0.1067	34.4463	1.2581	129
Pupae	0.0013	0.2443	34.4441	3.8968	61
Total development	0.0006	0.1490	34.4493	2.1796	3

[a] Degrees of freedom.

The most commonly reported lower thermal threshold in the literature for *C. pomonella* is 10° C. Using this value for comparison, the average number of degree-days required to complete development of the egg, larval, and pupal stages are 93.87° D, 280.62° D, and 256.93° D, respectively; the mean duration of total development is 631.42° D. Glenn (1922) presented data showing that an average of 645.00° D (base 10° C) were required for total development. In our study, the average number of degree-days from newly emerged larvae to adults was 537.55° D (base 10° C), a value similar to other studies (all base 10° C): 552.78° D (Glenn 1922), 494° D (Williams & McDonald 1982), 514° D (Rock & Shaffer 1983).

The average number of days for the total developmental period was estimated as the sum of the means for the egg, larval, and pupal stages. These data are plotted in Fig. 1 along with the range of observed values. Low or no survival at 34.4° C indicates that high temperature can inhibit *C. pomonella* developmental rate. A nonlinear function based on Logan's model (Logan et al. 1976) was used to describe the rate-temperature relationship (Fig. 1). The parameter estimates for each life stage are given in Table 3. For total development, the calculated lethal maximum temperature with 100% mortality was 34.45° C; the fastest rate of development was calculated to occur at 30.82° C. In contrast with the linear model, Logan's model exhibits a rapid decline at temperatures >31° C and also fits the data well in the intermediate temperature range.

Linear models of development have become widely used in practice because they have worked well for a wide variety of insects, they are easily modified (e.g., adding an upper thermal threshold), and their parameters are easily estimated from developmental data. Our study is significant because not only are the intermediate temperatures examined, but also temperatures at the upper and lower thermal limits of development. When a nonlinear function is fit to our data, a more complete description of the developmental rate curve of *C. pomonella* is presented. Air temperatures exceed 31° C almost daily during July through September in most regions of California where *C. pomonella* is found (University of California 1983) and use of this nonlinear model should improve prediction of immature development during these summer months.

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Received 3 December 1990; accepted 12 February 1991.